

Aquatic invertebrates of pit gnammas in southwest Australia

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Despite numerous studies on pan gnammas (rock pools) in recent years, the deeper, less-ephemeral pit gnammas remain virtually unknown except for their geomorphology. This study examined 50 pit gnammas in the Wheatbelt and adjacent Goldfields over 2010–2012 and found 82 taxa of invertebrates rich in insect variety but dominated numerically by a few crustaceans. Mean momentary species richness per pool averaged 8.2 (range 1.5–16.2), with more in larger pools and some clumped pools, and fewer in pools covered by rock slabs or with water flow through them. Pools across the study area showed a minor change in species composition from the northwest to south. In a comparison with pan gnammas, the distinctive physicochemical environment of pit gnammas is also largely determined by their location on granite outcrops, but their differing history and origins and hence hydrological environment have resulted in major differences in their invertebrate fauna. Pans are more species rich than pits, and have many endemic species, mainly crustaceans, but also a few insects, adapted to the regularly desiccating environment and subjected to strong UV rays. Fluctuating climates over millennia coupled with poor dispersal have promoted speciation among these crustaceans. By contrast, the more persistent pit gnammas support eurytopic species mostly easily dispersed, though two species of the clam shrimp *Lynceus* are characteristic.

KEY WORDS: Cladocera, gnammas, *Lynceus*, hydrology, insects, Ostracoda, physicochemical environment.

INTRODUCTION

Early studies of some gnammas on granite outcrops in the southwest of Western Australia recognised the interesting biological adaptations to living and surviving desiccation in these pools with their short hydroperiods and long periods of dryness. These included autecological studies by Edward (1968, 1989) and Jones (1971, 1974) on dipterans, especially *Paraborniola tonnoiri*, and taxonomical studies such as Fairbridge (1945), Cranston & Edward (1987), Frey (1998), Smirnov & Bayly (1995), Benzie & Bayly (1996), Hendrich & Fery (2008), Zofkova & Timms (2009) and Timms (2013b) on various invertebrates specific to rock pools. Later, community ecology with particular reference to the rich diversity of invertebrates was investigated (Bayly 1982, 1997; Pinder *et al.* 2000; Timms 2006; Jocqué *et al.* 2007a). There has also been considerable effort on similar pools overseas (Jocqué *et al.* 2007b, 2010a; Vanschoenwinkel *et al.* 2009) often with particular reference to interactions between faunal elements (Pajunen & Pajunen 1993; de Roeck *et al.* 2005; Jocqué *et al.* 2010b). It is now recognised that the fauna of gnammas of southwestern Australia is the most diverse of any inland rock pools anywhere, and with an array of adaptations and faunal interactions (Jocqué *et al.* 2010a).

However these comments apply only to the common shallow pan gnammas. The deeper pit gnammas (Twidale & Corbin 1963), with longer hydroperiods and generally shorter periods of dryness, have hardly been studied (Bayly 2002). One on Dingo Rock near Wongan Hills was included in the Pinder *et al.* 2000 study (A Pinder pers. comm. 2012); Bayly (1997) studied one on

War Rock near Morewa; Zofkova's (2006) work on the phylogeography of the pea shrimp *Lynceus* centred on species in pit gnammas in the Wheatbelt; and there is ongoing work on their ostracods (S Halse & K Martens pers. comms. 2011) and *Lynceus* (Timms 2013a). The geomorphology of pit gnammas is more complex than that of pan gnammas (Twidale & Vidal Romani 2005; Timms 2013b), but to date it seems their ecology is simpler (i.e. fewer species, fewer endemics, no special adaptations).

Pan gnammas in the Wheatbelt and adjacent Goldfields of southwestern Australia support a rich aquatic fauna dominated by crustaceans many of which are endemic to them (Bayly 1982, 1997; Pinder *et al.* 2000; Timms 2006; Jocqué *et al.* 2007a). This fauna is adapted to a distinct hydrological environment of filling in winter and drying in summer, and diversified by refugial response to a long history of climatic fluctuations (Pinder *et al.* 2000). At the local scale, community composition is affected by gnamma size, bigger pools having more species (Vanschoenwinkel *et al.* 2009), and density of pools on an outcrop and nearness to other rock outcrops expressed by enhancing dispersion when other pools are close by (B Vanschoenwinkel pers. comm. 2010). Also climatic gradients are another determinant of community structure, so that species richness decreases northwards and northwestwards with less reliable and shorter fillings of the gnammas (Timms 2012a, b). The ultimate restriction is seen in the depauperate fauna of desert pipe gnammas (another type of gnamma which are deep narrow shafts of water in non-granitic rocks) in eastern Western Australia with their small surface areas and extreme isolation greatly diminishing the arrival and survival of dispersers (Bayly *et al.* 2011). The third major type of rock waterhole are pit gnammas that are generally deeper, hemispherical in profile, less common

and more isolated and importantly not so closely tied to the seasonal hydrological pattern characteristic of pan gnammas (Timms 2013b). Their aquatic fauna would be expected to be not so specialised, not so diverse, nor affected as much by climatic gradients; in fact more akin to the fauna of any small waterbody regionally. Size would be expected to greatly influence species richness and there may be some influence of relative isolation on faunal composition.

In the past, pan and pipe gnammas have been characterised by the number of species they support (species richness) and their species composition. Multivariate analysis is increasingly being used to differentiate metacommunities (Timms 2012a, b). All analyses rely upon comparative sampling effort, something difficult to achieve for small temporary habitats. The third major type of gnammas, the deeper less-ephemeral pit gnammas, have not been studied, either in their general limnological features or in their faunal composition. The aims of the present study are to characterise the limnology of these pit gnammas in the southwest of Western Australia with special reference to assessing invertebrate communities and the major factors which influence species richness and community structure. This will be done in the context of comparison with the more common pan gnammas.

METHODS

Pit gnammas are sparsely distributed across southwestern Australia, with most granite outcrops lacking them or having only one or two, as opposed to numerous pan gnammas on most (Timms 2012a, b). Fifty of the 80 gnammas known to the author in the northern and eastern Wheatbelt and adjacent Goldfields (Timms 2013b) were chosen for limnological study (Figure 1). Choice of study gnammas was not random, but based on accessibility, background knowledge on each, and achieving a variety of sizes, geomorphic types and

district locations. Each was visited four to five times from October/November 2010 to August 2012 initially covering drought conditions then more normal seasonal conditions in July to September 2011 and August 2012. This enabled most to be seen dry, partly filled and completely filled, and all were sampled when water was present at four or five times.

On each visit a water sample was taken to determine conductivity in $\mu\text{S}/\text{cm}$ with an ADWA332 conductivity meter and turbidity was measured in a Secchi disc tube calibrated in Nephometric Turbidity Units (NTU). Depth was determined with a stout tape measure and when a pit was deemed full its length and width measured and volume was calculated (Timms 2013b). On the September 2011 trip, pH was determined with Hanna HI8924 meter. In the calculation of mean pHs, the logarithmic scale was first converted to arithmetic values via antilogs, averaged and then converted back to log values. Various geomorphic types were identified (Timms 2013b), but pertinent to this study were those on waterways—the lotic potholes. All others were considered lentic environments, though the plunge pools experienced significant flushing at times. Also some still had covers remaining from the days when indigenous folk placed covers on gnammas important to them for water supply (Appendix 1).

To sample the fauna, a dip net of 1 mm mesh and 25 cm wide, 20 cm high and 30 cm deep supported on a D frame and carried on a 1.8 m handle was used to catch macroinvertebrates for five minutes and a plankton net of mesh 159 μm , 25 cm wide, 15 cm high and 90 cm long and also carried on a handle 1.8 m long was used to catch zooplankton in the water column for one minute. Species accumulation per unit effort was not assessed, but experience strongly suggested almost all dip-netted species present in small gnammas ($V < 0.5 \text{ m}^3$) were caught in the first minute, similarly for medium-sized gnammas ($V = 0.6\text{--}5 \text{ m}^3$) in three minutes, and large gnammas ($V > 5.1 \text{ m}^3$) in five minutes with some

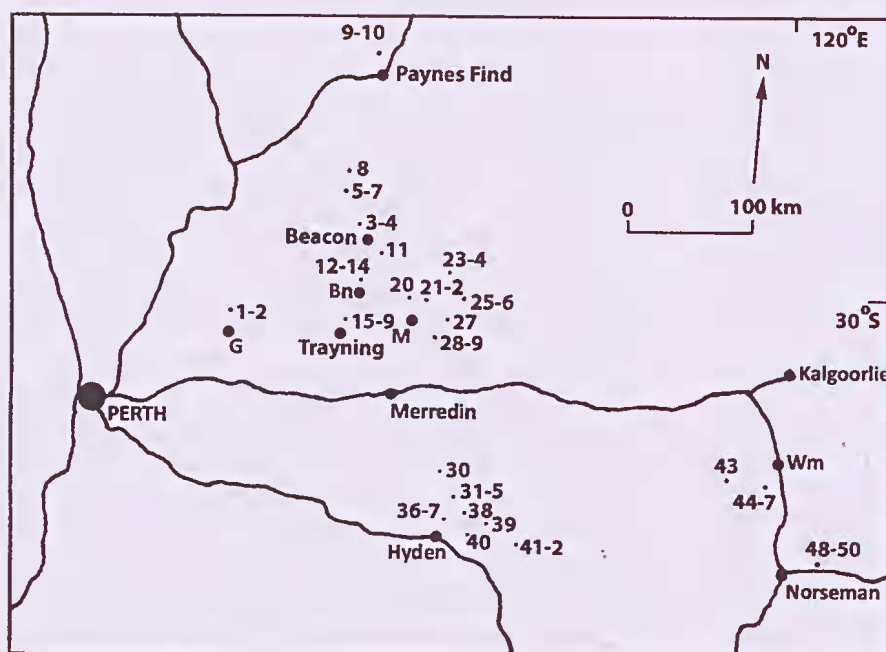


Figure 1 Map of southwestern Australia showing location of the 50 pit gnammas.

exceptions listed below. The pond net collected macroinvertebrates in the littoral, the open water and also the benthic infauna, though in large gnammas wider than 3 m and deeper than 1.5 m (e.g. Weira Gnamma) benthic sampling was inefficient, and in gnammas deeper than 2 m (e.g. Beringbooding North) it was logistically impossible to collect benthic infauna species at all. It is not known how inefficient this sampling was as there were no large gnammas in this series where sampling can be claimed to be truly efficient. Macroinvertebrates were sorted alive in a white tray, and representatives of all species caught were preserved in alcohol for later identification, and the remainder returned alive to the pit, together with all tadpoles caught. The whole zooplankton collection was preserved in alcohol for later study. For small gnammas ($V < 0.5\text{m}^3$), much smaller nets of the same meshes were employed for the same time periods.

The 50 pits were arranged into five groups of 9–11 pits each, according to district (northwest, north, northeast, south, east) (Figure 1; Appendix 1), but sometimes on landscape factors (e.g. the two Forestiana pits are close to most members of the south series, but are included with the east series as all the latter are in unfarmed scrub and woodland).

Relationships between these series and between them and pan gnammas in four of the five districts were investigated using PRIMER (v5) (Clarke & Gorley 2001).

To make the data as extensive and comparative as possible, 45 sets of presence/absence records were assembled from 9–11 pit gnammas in the five districts. For pan gnammas, data in Timms (2012a, b) was taken from 10 gnammas on Bullamanya Rock (6, (northwest), Yanneymooning Rock (7, northeast), Hyden Rock (8, south) and three rocks near Norseman (9, east). In the first three of these rocks data were accumulated from visits in June, July, early August, late August and September to give 45 sets; for the Norseman rocks to get 45 sets the three sets of 10 had to be multiplied by 1.5 as there was only one visit to these three rocks. While data assembly is somewhat heterogeneous the aim was to have a similar number for each group based on as many samplings as possible. Species which occurred only once in all nine groupings were ignored as they do not contribute to similarities.

The relationship between pit gnamma size and mean momentary species richness was tested using linear regression, while statistical differences between some gnamma types and their mean momentary species richness was investigated using one-way ANOVAs.

RESULTS

Physicochemical features

Morphometrics of the pit gnammas are examined in detail in Timms (2013b), but it is pertinent to note here that there is a large range in the size of the pits from a volume of 0.04m^3 to 110m^3 (Appendix 1), with a mean of 6.18m^3 and a median of 0.98m^3 . Though all contained fresh water, there was likewise a large range of mean conductivities from 39.3 to $587.2\ \mu\text{S}/\text{cm}$, with a mean value of $149.7 \pm 106.1\ \mu\text{S}/\text{cm}$ and a median of 115.2

$\mu\text{S}/\text{cm}$. Again the values were skewed with most between 51 and $150\ \mu\text{S}/\text{cm}$ (Figure 2a). The three exceptionally high values in Wattoning, Twine Shrub and Buldania West pits (Appendix 1) were for gnammas that apparently rarely overflowed. Contrawise, many of the lowest values were in pits that were covered (Whealers at $39.3\ \mu\text{S}/\text{cm}$) or on waterways (Cave Rock at $69.6\ \mu\text{S}/\text{cm}$). Conductivities in many pit gnammas varied widely between visits. Large, apparently permanently inundated gnammas exhibited the least variability in conductivities (e.g. Beringbooding North 131 – $338\ \mu\text{S}/\text{cm}$; Weira 43 – $153\ \mu\text{S}/\text{cm}$) while many small gnammas which were sampled when almost dry and again when full had the widest variations in conductivity (Trayning Mid 66 – $540\ \mu\text{S}/\text{cm}$; Yellari North 34 – $424\ \mu\text{S}/\text{cm}$).

Gnamma waters were generally clear with 74% of values < 20 NTU and 42% < 10 NTU and with a mean value of 18.8 NTU for all 50 sites (Figure 2b; Appendix 1). A few gnammas occasionally had algal blooms increasing turbidity and some like Yellari North and Buldania East (mean turbidities 108.7 and 91.6 NTU) had major algal blooms on all visits, or most visits (Oak Flat West 37 NTU). Only a few gnammas had turbidities that seemed to be largely influenced by turbid runoff, these being Wiera at 49.6 NTU, Higgensville North at 41.2 NTU, Higgensville Mid at 41.2 NTU and the two Willogyne gnammas at 30.8 and 40.0 NTU. When these eight are ignored the mean turbidity reduced to 8.2 NTU.

All gnammas were neutral to alkaline (pH range 7.0 – 8.8 , mean 7.49) on the September trip in 2011.

Biological features

Eighty-two taxa were found in the 50 gnammas, many species occurring sporadically and many rarely (Table 1). Sixteen percent of species occurred just once, 34% were found up to three times, and 49% of species occurred five times or fewer. The most widespread and common species were, in order: ostracod *Cypricercus* spp., the boatman *Agraptocorixa parvipunctata*, the dytiscid *Sternopriscus multimaculatus*, the midge *Chironomus tepperi*, the copepod *Boeckella triarticulata*, the boatman *Micronecta gracilis*, the pea shrimp *Lynceus magdaleanae*, the cladoceran *Moina australiensis* and the backswimmer *Anisops thienemanni*. If this list is extended to include all those species with more than 25 records, then of the 23 species, 16 are insects and 7 crustaceans. Of the full list, there are 54 insects, 25 crustaceans, 4 molluscs, 3 turbellarians, 3 rotifers, 2 arachnids and 1 oligochaete.

Distribution of species across the study region is uneven, even for common species (Table 1). Most noticeable is the absence or major restriction of many species in the south plus east districts. Examples include *Lynceus baylyi*, *Moina australiensis*, *Boeckella triarticulata* and *Antiporus gilberti*. The southern district, which includes six gnammas on Twine Rock has a restricted fauna, with *Lynceus magdaleanae*, many beetles, bugs and molluscs comparatively uncommon (Table 1) But other species such as *Mesocyclops* cf. *notius*, *Hemicordulia tau*, *Anisops hyperion* and *Chironomus alteruans* were unusually common (Table 1).

Multivariate analysis of each gnamma's fauna showed many of the gnammas in each group were closely allied and furthermore suggested a minor trend from

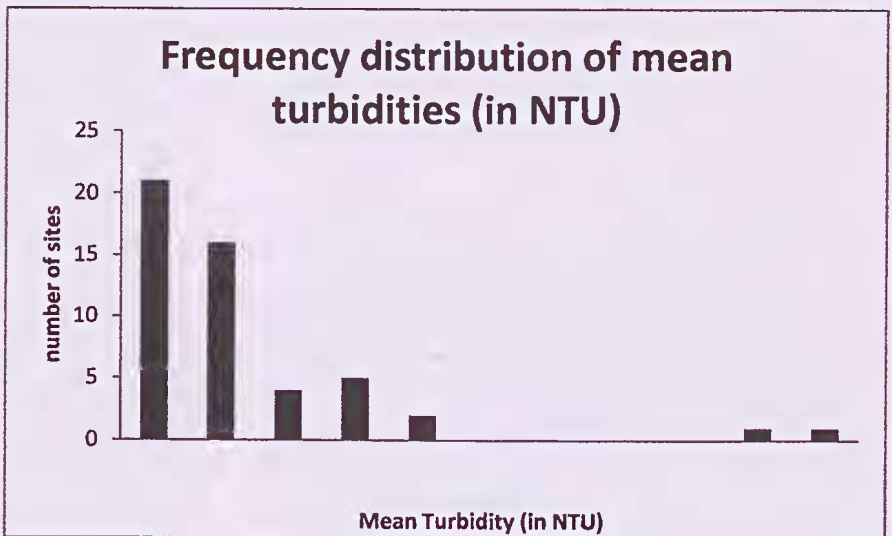
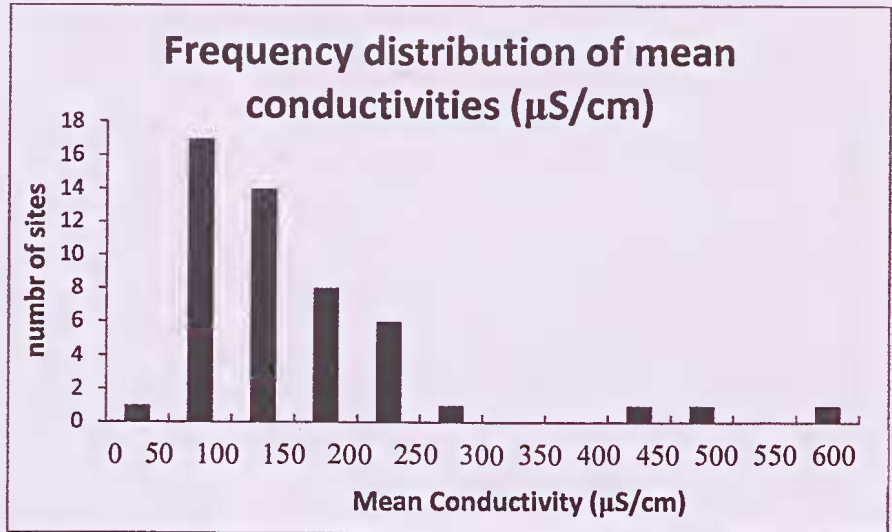


Figure 2 (a) Frequency distribution of mean conductivities (in $\mu\text{S}/\text{cm}$). (b) Frequency distribution of mean turbidities (in NTU).

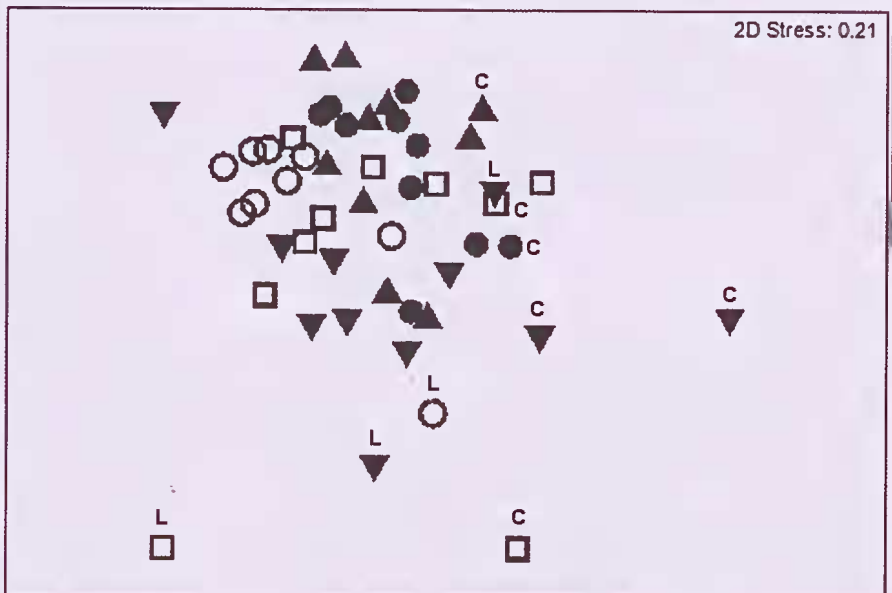


Figure 3 nMDS plot of relationships of invertebrate communities in the 50 gnammas. \blacktriangle , 10 gnammas in the northwest district; \bullet , 10 gnammas in the northdistrict; \circ , 9 gnammas in the northeast district; \blacktriangledown , 11 gnammas in the south district; \square , 10 gnammas in the southeast district; C, covered gnammas; L, lotic gnammas.

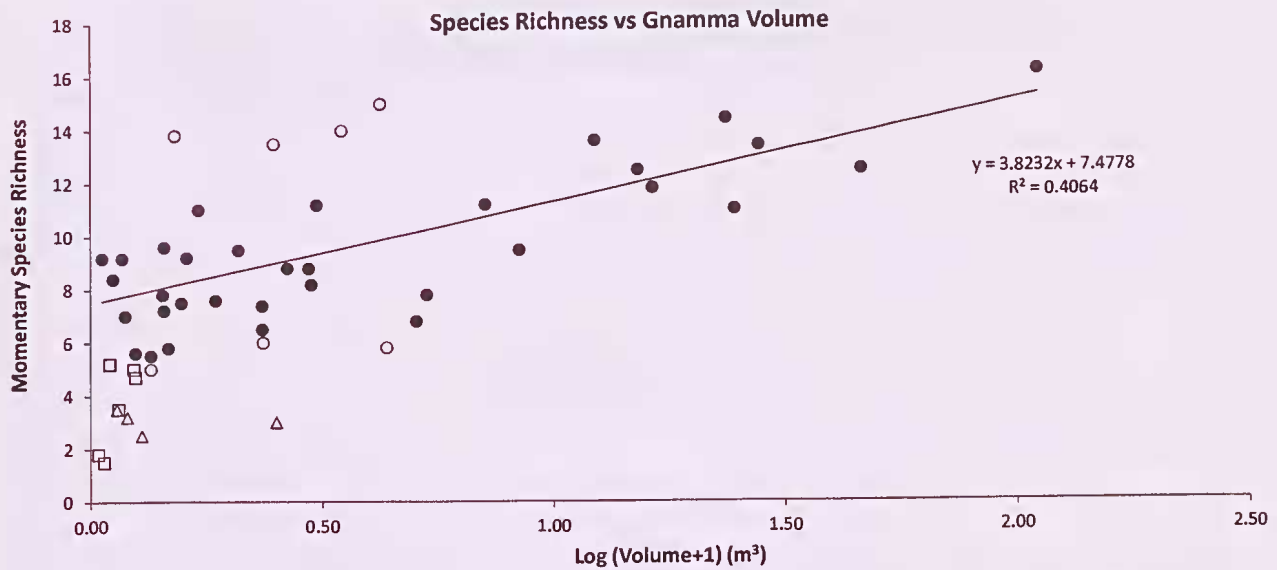


Figure 4 Relationship between mean momentary species richness and gnamma volume. ●, normal gnammas; ○, normal gnammas well removed from trend line; □, covered gnammas; △, lotic gnammas.

northwest to south, though the remote east gnammas clumped with north gnammas (Figure 3). One-way anosims of all possible pairings between the five districts showed differences between each were mostly significant at 5% ($r = 0.112-0.406$) for all except the northwest and north pair ($r = 0.009$) and the south and east pair ($r = 0.068$). This nMDS plot also suggests some gnammas lie outside the main clump; these are the covered and lotic gnammas discussed later.

Larger gnammas, by volume, supported more species, the correlation ($r = 0.4064$) being significant at $P < 0.001$ for the 40 normal gnammas (i.e. those uncovered and lentic) (Figure 4). The regression line for this relationship is highly significant ($P < 0.000001$). This is despite some very large gnammas not being sampled effectively and hence not as speciose as might expected. The impact of the 'missing' species on the relationship at the large end of the relationship could not be tested easily, but at the other end of the scale some of the large variation in species richness is testable. The apparent negative influence of gnamma cover plates and location on a waterway is testable. For the unusual covered and lotic gnammas there was no relationship between species richness and size (Figure 4), and when compared respectively to covered and lentic pools of the same size, both showed a significantly reduced fauna (Figure 5a, b). All pairings are significantly different at $P = 0.05$ or better (Table 2).

Other gnammas somewhat different from the normal (i.e. uncovered and lentic) gnammas are shown in open circles on Figure 4. There are four with mean species richness well above what might be expected for their size and at least three with species richness below expectations (there are more slightly less extreme than these, but there is no easy explanation for their deviation). Three of the four above the line are in the Trayning series, a closely spaced series of five gnammas at about 1–5 m intervals along a rock joint (Timms 2013b) and the other one is Buldania East Gnamma, part of a

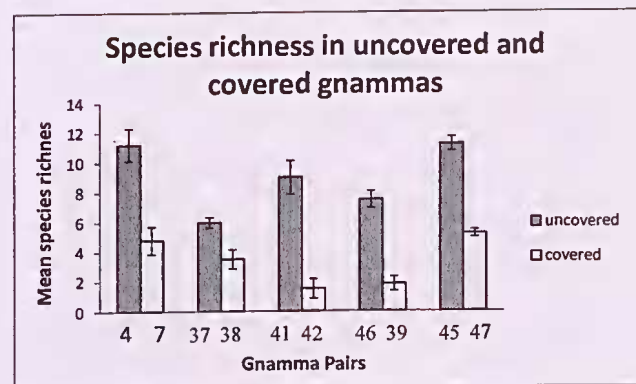
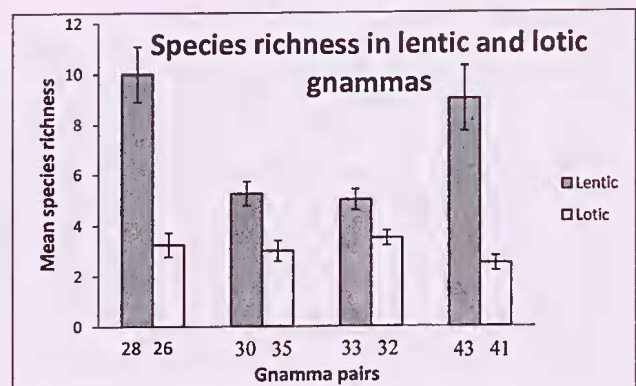


Figure 5 (a) Species richness in paired lentic and lotic pit gnammas. (b) Species richness in paired uncovered and covered pit gnammas.

group of three gnammas about 30–40 m apart. The inference here is that closely spaced gnammas accumulate more species because dispersal is more efficient over short distances. However the effect was not significant when tested in a best case scenario [five Trayning pits in a row less than 30 m end to end and averaging 2.1 m apart compared to five other pans (Oak

Table 1 Number of records of invertebrates in the 50 pit gnammas.

Taxa	Northwest	North	Northeast	Hyden	Norseman	Total
Turbularia						
unident. planarian 'grey'	1	-	3	-	2	6
unident. planarian 'black'	2	1	1	-	-	4
unident. planarian 'flat green'	4	-	-	-	5	9
Oligochaeta						
<i>Limnodrilus hoffmeisteri</i>	3	8	6	1	-	18
Rotifera						
<i>Asplanchna</i> sp.	-	1	4	-	-	5
<i>Brachionus</i> spp.	1	-	6	1	-	8
<i>Keratella australis</i>	-	-	5	-	-	5
Branchiopoda						
<i>Branchinella affinis</i>	1	-	-	-	-	1
<i>Lynceus baylyi</i>	24	26	-	-	-	50
<i>Lynceus magdalenae</i>	11	8	26	5	17	67
<i>Paralimnadia badia</i>	-	-	-	-	4	4
<i>Eulimnadia ?dahli</i>	1	-	-	-	-	1
<i>Caenestheriella nuriae</i>	2	-	-	-	-	2
<i>Triops australiensis</i>	1	-	-	-	-	1
Cladocera						
<i>Daphnia jollyi</i>	-	-	-	-	1	1
<i>Daphnia carinata</i>	6	3	6	-	4	19
<i>Simocephalus acutirostratus</i>	1	-	-	-	-	1
<i>Moina australiensis</i>	16	22	13	8	7	66
<i>Alona</i> spp.	2	-	2	1	-	5
Copepoda						
<i>Boeckella opaqua</i>	-	-	-	-	4	4
<i>Boeckella triarticulata</i>	20	15	33	1	3	72
<i>Mesocyclops cf notius</i>	10	4	7	13	4	38
<i>Macrocyclus</i> sp.	-	-	3	-	-	3
Ostracoda						
<i>Bemmelongia</i> sp.	1	-	1	-	-	2
<i>Candonocypris novaezealandiae</i>	1	5	4	6	2	18
<i>Cyprretta baylyi</i>	-	-	3	-	2	5
<i>Cypricercus</i> spp.	22	28	12	25	19	106
<i>Heterocypris</i> sp.	12	10	5	1	5	33
<i>Ilyodromus amphicolis</i>	2	3	-	2	2	9
<i>Ilyodromus</i> spp.	-	1	1	-	-	2
<i>Sarscypridopsis</i> sp.	1	-	1	-	-	2
Decapoda						
unident. Parastacidae	-	-	-	1	-	1
Odonata						
<i>Austrolestes analis</i>	-	-	3	-	-	3
<i>Ischnura heterostrica</i>	4	1	5	1	3	14
<i>Hemiaux papuensis</i>	3	-	5	-	1	9
<i>Hemicordulia tau</i>	2	4	16	20	4	46
<i>Orthetrum caladonicum</i>	5	4	7	8	4	28
<i>Trapezostirma lewii</i>	-	-	2	-	-	2
Ephemeroptera						
<i>Cloeon</i> sp.	1	-	-	-	1	2
Hemiptera						
<i>Micronecta gracilis</i>	15	14	21	11	9	70
<i>Agraptocorixa parvipunctata</i>	22	28	24	14	13	101
<i>Sigara mullaka</i>	-	-	-	-	1	1
<i>Anisops gravis</i>	3	10	21	6	8	48
<i>Anisops hyperion</i>	4	5	3	12	9	33
<i>Anisops stali</i>	9	4	15	3	2	33
<i>Anisops thienemanni</i>	7	11	22	11	11	62
Trichoptera						
<i>Triplectides ?australis</i>	4	1	13	7	4	29

Timms: Aquatic invertebrates of pit gnammas, WA

Taxa	Northwest	North	Northeast	Hyden	Norseman	Total
Coleoptera						
<i>Allodessus bistrigatus</i>	4	5	5	-	2	16
<i>Allodessus larvae</i>	3	2	-	-	2	7
<i>Antiporus gilberti</i>	13	10	16	4	7	50
<i>Antiporus larvae</i>	10	13	13	2	4	42
<i>Berosus</i> spp. (inc. <i>B. nutans</i>)	12	2	3	1	4	22
<i>Berosus larvae</i>	2	-	1	-	2	5
<i>Cybister tripunctatus</i>	-	-	1	-	-	1
<i>Enochrus maculipes</i>	-	-	1	3	1	5
<i>Eretes australis</i>	8	7	8	2	6	31
<i>Eretes larvae</i>	1	-	-	2	1	4
<i>Hyphydrus elegans</i>	2	3	12	2	-	19
<i>Hyphydrus larvae</i>	-	3	1	2	1	7
<i>Lancetes lanceolatus</i>	1	1	1	-	2	5
<i>Lancetes larvae</i>	-	-	-	-	2	2
<i>Limnoxenus zelandicus</i>	3	4	2	-	2	11
<i>Limnoxenus larvae</i>	-	2	1	-	-	3
<i>Megaporus howitti</i>	-	-	1	-	-	1
<i>Megaporus larvae</i>	-	-	1	-	-	1
<i>Necterosoma darwini</i>	1	3	7	-	-	11
<i>Necterosoma larvae</i>	2	-	-	-	-	2
<i>Rhantus suturalis</i>	3	3	2	3	-	11
<i>Rhantus larvae</i>	-	2	-	1	-	3
<i>Sternopriscus multimaculatus</i>	21	29	18	13	19	100
<i>Sternopriscus larvae</i>	2	3	4	3	2	14
Diptera						
<i>Chironomus alternans</i>	3	8	1	10	3	25
<i>Chironomus occidentalis</i>	1	-	-	-	-	1
<i>Chironomus tepperi</i>	19	14	20	16	14	83
<i>Cryptochironomus</i> sp.	1	-	4	2	3	10
<i>Dicrotendipes</i> sp.	-	-	-	2	-	2
<i>Paraborniella tonnoiri</i>	-	-	3	1	1	5
<i>Polypedilum nubifer</i>	-	-	1	-	-	1
<i>Procladius</i> sp.	2	-	-	-	-	2
<i>Tanytarsus</i> sp.	-	1	4	-	1	6
unident. Chironomidae	2	1	2	2	1	8
<i>Aedes occidentalis</i>	13	15	6	16	2	52
<i>Aedes notoscriptus</i>	-	-	-	4	-	4
<i>Anopheles annulipes</i>	-	-	-	1	-	1
<i>Culex australicus</i>	-	-	-	1	-	1
unident. Ceratopogonidae	4	4	7	3	3	21
unident. Stratiomyidae	6	2	6	-	1	15
Acarina						
unident. Eyladidae	1	4	3	1	-	9
unident. Hydrachnidae	-	1	2	-	-	3
Gastropoda						
<i>Glyptophysa</i> sp.	-	-	-	1	-	1
<i>Isidorella</i> sp.	-	11	-	-	-	11
<i>Physa acuta</i>	-	-	12	-	6	18
Bivalvia						
<i>Musculium</i> sp.	-	3	4	-	-	7

Flat East, Oak Flat West, Yellari North, Yellari South, Remlap) of similar volume and much further apart (averaging 18 km) from adjacent pit gnammas]; mean CSR was 24.6 in the Trayning series and 19.2 in the comparison series but Student t was 0.1083 and not significant even at P = 10%.

The three below the regression line are Bullamania North, Bullamania South and Twine North, all plunge pits (Timms 2013b) and so subject to strong flowthrough

at times. The inference here is that sometimes these gnammas are subject to scouring and possible loss of species. There are no suitable controls to test this, but the effect is slight and unlikely to be significant.

While there is a high degree of similarity in faunal composition between the 40 normal gnammas and even the 10 unusual covered and lotic pans (Figure 3), pit gnammas support a fauna very dissimilar to that in pan gnammas (Figure 6). This is despite the comparison not

Table 2 Student t values for gnamma pairings in Figure 5.

Pairings	t value
Covered vs uncovered (Figure 5b)	
4 & 7	0.0035
37 & 38	0.0160
41 & 42	0.0020
46 & 39	0.0064
45 & 47	0.0007
Lentic vs lotic (Figure 5a)	
26 & 28	0.0012
35 & 30	0.0117
33 & 32	0.0240
41 & 43	0.0027

being perfectly matched (e.g. though numbers of each type are in groups of 10, sampling intensity is different and there are representatives of pans in only four of the five districts).

During the drought of 2010 and occasionally at other times, dead vertebrates (lizards, snakes, emus, kangaroos) were observed in 10 pits with multiple drownings in Yellari North, Quanta Cutting, Weira, Twine Mid, and Buldania East, all deep gnammas with steep sides. In fact such gnammas present a hazard to humans, so authorities have filled in some (e.g. at War Rocks via Morewa, and Dingo Rocks via Wongan Hills) or fenced others (e.g. Jibberding Rocks via Wubin, Moningarín gnammas via Cadoux, and one at Buldania Rocks), thus reducing the number of bigger, deeper gnammas available for study.

DISCUSSION

Physicochemical features

Many of the characteristic physicochemical features of pit gnammas are determined by their morphometry and relationship to their catchment, as for most waterbodies (Wetzel 1975). The majority have small catchments of exposed granites and hence incoming waters are of low salt content and clear. Exceptions occur when inflowing waters come from further afield and carry salts and solids. Deep impervious rock basins prevent loss of water and salts, so gnammas tend to act like rain gauges, losing water mainly by evaporation. Those with covers often have lower conductivities as a cover slows water loss, so in past times when indigenous people placed covers over many gnammas (Bayly 2002; Twidale & Vidal Romini 2005), it is possible conductivities in many more pit gnammas were lower, and fluctuations less. Under present climatic conditions in southwestern Australia many gnammas occasionally overflow and so lose some accumulated salts. Lotic potholes along waterways also tend to have lower conductivities as in these no accumulation of salts is possible, except briefly in droughts. Also, gnammas like Beringbooding North that hold water permanently have lower fluctuations in conductivities than those like Trayning Mid which dry



Figure 6 nMDS plot of relationships of invertebrate communities in the 50 pit gnammas arranged in five groups and four groups of pan gnammas. 1, northeast district; 2, north district; 3, northwest district; 4, south district; 5, southeast district; 6, Bullamanya Rock; 7, Yanneymooring Rock; 8, Hyden Rock; 9, three rocks near Norseman.

seasonally. Data on conductivities are too infrequent to analyse for seasonal changes from filling to drying, but undoubtedly there is concentration of salts as pit gnammas dry, a fact noted by Bayly (2001) for a rockhole in central Australia and also in pan gnammas in the Wheatbelt (Timms 2012a). Despite some higher values persistently or temporarily in these gnammas, water is always fresh and of characteristically low salinity which is important for the survival of freshwater invertebrates, given most of the surrounding waters on the plains are now saline. This feature they share with the pan gnammas on similar granite outcrops, though average conductivities are a little higher (Pinder *et al.* 2000; Timms 2012a).

Also shared with pan gnammas is the clear waters in most pit gnammas, though they are not crystal clear as in almost all pans [mean of 3.1 NTU for 9 pans (Pinder *et al.* 2000) compared with a mean of 9.2 NTU for 42 pits unaffected by extraneous factors]. Exceptions occur when inflowing water is sourced from non-granitic catchments and slugs of nutrients added when large vertebrates fall in and die, as observed during the 2010 drought. So while nutrients are low in pan gnammas (Pinder *et al.* 2000) it seems they could be higher in at least such pits, with the consequence of persistent algal blooms and opaque waters.

For the present 50 pit gnammas the pH ranges from 7.0 to 8.8 with a mean of 7.49. Concordantly, the pH of the sole pit gnamma [War Rock (b)] examined by Bayly (1997) was 7.9. In contrast, the pH of the 34 pan gnammas other than Coragina (a) (Bayly 1992) studied by Bayly (1997) ranged from 4.6 to 7.3 with a mean of 6.49. There is clear evidence, therefore, that the water of pit gnammas is generally alkaline and that of pan gnammas typically acidic. This suggests pit gnammas are less influenced by their acidic granitic base than pans perhaps due to separation by abundant bottom sediment (Timms 2013b) and/or in some cases due to salts from larger catchments/accumulated vertebrate bodies.

Biological features

Cumulative species richness for pools in a defined study area depends on many factors particularly the number of sampling occasions, the number of pools sampled, taxonomic resolution and the size of the area sampled, thus making meaningful comparisons between various studies difficult. This study of pit gnammas across the Wheatbelt and into the Goldfields recorded 82 species whereas Pinder *et al.* (2000) found 230 species in pan gnammas and associated waterholes in the same area, but from more pools and with wider and better taxonomic resolution. In an intensive study of 10 pans each on three rocks in the Wheatbelt, momentary species richness (MSR) averaged 30.75 species on Mt Madden, 26.5 species on Hyden Rock and 29.5 species on Yanneymoon Rock (Timms 2012a). The highest figures for MSR in this study were 16.2 in Beringbooding North and 14.4 in Melancobbing, both large pits, with an average value of 8.2 for the 50 pits, as there were many small gnammas with few species. The conclusion then is pan gnammas support more species than pit gnammas, though the exact difference is unknown. In both types of gnammas, bigger sites support more species [Vanschoenwinkel *et al.* (2009) for pans and this study on pits], but the effect of rainfall gradients on richness in pans (Timms 2012a, b) is not seen in pits. In pit gnammas variation in size and some habitat factors such as presence or absence of a cover and location on a waterway are the most important determinants of MSR, and these act inconsistently across the Wheatbelt. It is possible that many pit gnammas now are more species rich, especially of mobile insects, since European settlement as in the past Aborigines covered many with rock slabs or vegetation to reduce water loss (Bayly 2002), but in reality reducing access to dispersing invertebrates.

The only other studies on deeper gnammas have been by Bayly (1997) on War Rock in the Northern Wheatbelt, Bayly *et al.* (2011) on pipe gnammas in laterite (which provide a similar habitat as pit gnammas) in the Victoria Desert of southeastern Western Australia and Bayly (2001) on a pit (canoe variety) 90 cm deep in central Australia. Bayly (1997) with one visit found just four species in the War Rock pit, but significantly two of these, *Boeckella triarticulata* and *Lynceus* sp. rarely occurred in all his pan gnammas. The author has visited this gnamma three times and found 20 species cumulatively including these two non-pan species (and thus showing the value of multiple samplings, but not included in this data set as there was not the adopted standard of four samplings). Those gnammas isolated in the Victoria desert averaged 4.6 species and the central Australia pit had 9 species after 10 samplings, all somewhat fewer than the present pit gnammas of similar size. As Bayly *et al.* (2011) noted, isolation plays a major role in these desert pools. Some of the present series of pit gnammas are relatively close together, and moreover near pan gnammas with which they share many insects (see later), so they could have more species than normal because of a nearby source of dispersers. This was observed in the Trayning gnammas and one Buldania gnamma (Figure 4).

Two of the species, *Limnodrilus hoffmeisteri* and *Physa acuta* are exotic, often occurring in adjacent gnammas (e.g. *P. acuta* occurs in many gnammas in the northeast

district), but neither are widespread and both have notable absences (*P. acuta* in the north and northwest; *L. hoffmeisteri* in the east and almost all of the south districts). Hardly any species are endemic to the pit gnammas, exceptions being the pea shrimps, *L. baylyi* and *L. magdaleanae* (previously misidentified as *L. macleayanus* in Timms 2006; Zofkova & Timms 2009 and Bayly *et al.* 2011) which occur only in gnammas, but also outside the study area (Timms 2013a). There are also some new ostracod species in the genera *Bennelongia* and *Heterocypris*, but some of these are not specific to pit gnammas (K Martens pers. comm. 2013)

This is the first time a sphaeriid bivalve has been found in a gnamma: *Musculium* sp., probably *M. keudricki*, the only species recorded in Western Australia. It is uncommon, found only in a few rivers along the southwest coast (Korniushin 2000) and once in the Wheatbelt (A Pinder pers. comm. 2013). Now there are three more locality records from the Wheatbelt, Trayning North, Melancobbing and Weira gnammas, all in the north and northeast districts. The response of this species to desiccation is unknown (some sphaeriids can tolerate desiccation, others cannot: Burch 1975; Clarke 1981), but it is noteworthy that the only gnammas it was found in did not dry during the 2010 drought while all other gnammas in the north and northeast areas did. Also its occurrence in just three gnammas and lack of spread to the other nearby Trayning gnammas, may indicate poor dispersal ability. This is explained by waterfowl, their main vectors, being uncommon visitors to deeper rocky waterholes (B V Timms unpubl. data).

Comparison of pit and pan gnammas

Morphologically pit and pan gnammas are very different, pans being shallow saucer-like rock-holes and pits are deeper, generally hemispherical-shaped hollows (Twidale & Vidal Romani 2005; Timms 2013b). Both are formed by water rotting granite; in pans the rotting is directed horizontally along laminations while in pits the rotting is along a hemispherical front in homogeneous rock, but often directed by vertical joints. Their morphology confers very different hydrological regimes: pans fill seasonally for a few weeks to months, while pits are much longer, lasting many months to years. As noted above, because both are on exposed granite, conductivities are low, water is clear and mildly acidic to mildly alkaline, though water in pits is generally a little higher in salts, less clear and of higher pH than in pans. Their faunal composition and ecology are entirely different.

Insects are comparatively more species rich in pits than in pans, with 66% of taxa in pits and only 45% in pans (Pinder *et al.* 2000). However in both, crustaceans are the most common numerically, with pits dominated by *Cypricercus* spp., *Lynceus* spp and *Moiua australiensis* and pans dominated by *Boeckella opaqua*, *Branchinella longirostris*, *Paralimnadia badia*, *Ceriodaplnia* spp., *Daphnia jollyi*, *Macrothrix hardingi*, various chydorids, *Bennelongia* spp., *Cypretta baylyi*, *Ilyodronus* spp. and *Cypricercus* spp. (Timms 2012a, b). The large array of endemic crustaceans in pans (Pinder *et al.* 2000) is not repeated in pit gnammas with just two species of *Lynceus* (Timms 2013a) and possibly some endemic ostracods (K Martens pers. comm. 2013). The insects in pit gnammas are all widespread eurytopic species, as are almost all in pans,

though *Paroster baylyi* and *P. ursulae* are endemic to pans (Hendrich & Fery 2008) as are a few chironomids such as *Allotrissocladius* spp. and *Archaeociliclus* spp. (Edward 1989; Pinder *et al.* 2000). Almost all of the insects encountered in pits bred successfully there, as noted by immature stages seen, but fewer are successful in pans. At least in some cases in some years, exemplified by odonatans in 2010 (Timms 2012a), pans dry before the nymphs mature. The insects of pans are largely a subset of those in pits, with notable exceptions listed above, and all dispersing actively as adults. Probably many pit gnammas, especially bigger ones, act as reservoirs for flying species without resistant eggs (see below). The contention by Hendrich & Fery (2008) that their new species of *Paroster* survive pan desiccation by resistant eggs is almost certainly wrong given similar species of *Paroster* disperse into other pans as soon as they fill, breed and eventually leave (Timms 2012a). Crustaceans are advantaged by their resistant eggs so that they are preadapted to seasonally drying pans. Passive egg dispersal is not as efficient as active adult dispersal of insects (Hulsman *et al.* 2007; Vanschoenwinkel *et al.* 2007), so that during long periods of marked climatic changes in southwestern Australia, isolated populations of crustaceans speciated giving the multiple varieties and species in many genera seen in the pans today (Bayly *et al.* 2011, Pinceel *et al.* 2013).

Occasionally some pan species such as *Paralimnadia badia*, *Caenestheriella mariae*, and *Boeckella opaqua* are found in pit gnammas (Table 1), but this is explicable by flooding from surrounding pans. Sometimes species typical of pans such as *Parabornella tonnoiri* occur in pits; this can only be attributable to misplaced breeding events and unexceptional given this species is also known elsewhere from non-pan sites (Jones 1974). Finally, the three pit gnammas on Bullamanya Rock with their abundant *Chironomus tepperi*, could be a ready source for this species in the nearby pan gnammas on this rock where this species is unusually abundant (Timms 2012a). The same phenomena could well apply to insects in general when there are pit gnammas near a suite of pan gnammas, so that some of the insects seen in these pans could have a nearby source (Jocqué *et al.* 2007a).

Besides preadaptation to desiccation in the crustaceans, many species in pans also exhibit some physiological and behavioural adaptations to living in this stressful environment. Strong UV rays in the clear waters are counteracted by many with dark cutaneous pigments (e.g. *Paralimnadia badia*, *Daphnia jollyi*, *Macrotrix lardingi*, most chydorids) or red colouration internally (e.g. *Boeckella opaqua*). *Branclinella longirostris* tends to avoid the problem by typically staying close to the bottom during strong daylight (B V Timms unpubl. data). By contrast none of the crustaceans in the deeper pit gnammas have protective colouration. Some chironomids, particularly *Parabornella tonnoiri* are cryptobiotic in pans, thus enabling them to not only survive desiccation, but to emerge as soon after the pond fills and be the first chironomid to reproduce (Jones 1974; Timms 2012a). No ecological or physiological adaptations have been observed in pit species where they would be of no advantage, though it is possible the red *Lyneceus* seen in some pits have haemoglobin to enable respiration in possibly reduced oxygen at the bottom of pits with much organic matter.

CONCLUSIONS

The bare granitic rock catchments of pit gnammas result in their waters being of low salinity, and generally clear and slightly alkaline, similar to water in pan gnammas on similar rocks. The greater depth of pits compared with pans means pit gnammas as not as hydrologically restricted as pan gnammas which affects their fauna. First, special adaptations to short hydroperiods and strong UV light are not needed; second, climatic gradients are not so influential in species composition; third, access for dispersers is more restricted in pit gnammas because of their greater spacing and perhaps covering; fourth, perhaps surprisingly, speciation has been greater in pans than pits probably because their greater numbers on many isolated rock outcrops and specialised habitat provided ideal conditions for speciation in a fluctuating climate. By contrast pit gnammas are unremarkable, (except for their mode of origin) and unspecialised small pools widely spaced across the landscape.

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Appendix 1 Physical and chemical features of core pit gnammas.

Name	Nearest town	Coordinates	Volume m ³	Times visited	Mean conductivity \pm SE (μ mS/cm)	Mean turbidity \pm SE (NTU)	Cumulative species richness	Mean species richness \pm SE
Northwest District								
1	Oak Flat West	31° 08' 21"S; 116° 52' 46"E	1.95	4	146.2 \pm 24.9	37.5 \pm 30.8	19	8.8 \pm 1.4
2	Oak Flat East	31° 08' 20"S; 116° 52' 49"E	1.66	4	114.0 \pm 26.5	8.6 \pm 4.5	15	8.8 \pm 1.2
3	Yellari South	30° 19' 44"S; 117° 49' 58"E	6.12	5	76.4 \pm 16.2	29.5 \pm 10.8	15	11.2 \pm 1.1
4	Yellari North	30° 19' 44"S; 117° 49' 58"E	0.12	5	139.2 \pm 73.0	108.7 \pm 86.9	22	8.4 \pm 1.0
5	Washington South	30° 09' 06"S; 117° 34' 41"E	45.16	4	122.0 \pm 48.5	19.7 \pm 5.4	25	12.5 \pm 2.5
6	Washington Northwest ¹	30° 08' 52"S; 117° 34' 46"E	0.17	4	121.7 \pm 54.6	10.6 \pm 2.3	20	9.2 \pm 1.9
7	Washington Northeast ³	30° 08' 57"S; 117° 34' 41"E	0.25	4	156.0 \pm 44.9	17.5 \pm 10.7	12	4.7 \pm 0.8
8	Remlap North ²	30° 02' 04"S; 117° 37' 50"E	7.45	4	82.2 \pm 24.3	6.0 \pm 0.8	22	9.5 \pm 1.2
9	Bullamanya South ²	29° 09' 53"S; 117° 39' 36"E	1.36	5	77.6 \pm 13.5	3.7 \pm 0.5	18	6.0 \pm 0.6
10	Bullamanya North ²	29° 09' 52"S; 117° 39' 36"E	3.36	5	92.6 \pm 23.5	3.7 \pm 0.5	22	5.8 \pm 0.9
North District								
11	Wondoning Hill	30° 34' 36"S; 118° 04' 43"E	1.35	4	65.0 \pm 26.0	12.0 \pm 6.6	11	6.5 \pm 1.2
12	Cadigan North ³	30° 46' 53"S; 117° 52' 22"E	0.10	4	110.5 \pm 35.6	18.7 \pm 7.3	11	5.2 \pm 0.5
13	Cadigan Mid ²	30° 46' 54"S; 117° 52' 22"E	4.31	4	149.0 \pm 29.4	6.3 \pm 1.1	14	7.8 \pm 0.6
14	Cadigan South ²	30° 46' 54"S; 117° 52' 22"E	1.09	4	170.7 \pm 31.6	10.4 \pm 3.6	18	9.5 \pm 0.5
15	Trayning Far Southwest	30° 59' 29"S; 117° 50' 46"E	3.23	4	246.0 \pm 16.8	29.5 \pm 20.2	28	15.0 \pm 1.8
16	Trayning Southwest	30° 59' 29"S; 117° 50' 46"E	0.61	4	57.5 \pm 10.2	17.5 \pm 12.5	21	9.2 \pm 1.2
17	Trayning Mid ²	30° 59' 29"S; 117° 50' 47"E	0.52	4	241.5 \pm 107.6	12.2 \pm 7.3	28	13.8 \pm 2.8
18	Trayning Northeast ¹	30° 59' 28"S; 117° 50' 47"E	1.49	4	155.0 \pm 43.1	14.0 \pm 6.9	31	13.5 \pm 2.9
19	Trayning Far Northeast	30° 59' 28"S; 117° 50' 47"E	0.57	4	203.6 \pm 37.4	3.7 \pm 0.7	15	7.5 \pm 0.8
20	Wattoning	30° 46' 11"S; 118° 11' 14"E	0.35	4	587.2 \pm 138.9	4.4 \pm 0.6	14	5.5 \pm 0.6
Northeast District								
21	Willogyne North	30° 45' 59"S; 118° 16' 27"E	14.24	4	110.5 \pm 66.2	30.8 \pm 21.4	25	12.5 \pm 1.6
22	Willogyne South	30° 45' 59"S; 118° 16' 27"E	15.39	4	151.5 \pm 77.3	40.0 \pm 22.2	27	11.8 \pm 1.2
23	Beringbooding North	30° 33' 31"S; 118° 29' 42"E	110.00	5	222.6 \pm 35.5	20.5 \pm 6.1	32	16.2 \pm 1.5
24	Beringbooding Southwest	30° 33' 38"S; 118° 29' 35"E	23.60	5	156.8 \pm 34.0	6.8 \pm 0.8	20	11.0 \pm 1.7
25	Melancobbing	30° 40' 12"S; 118° 32' 21"E	22.62	5	115.2 \pm 32.5	8.0 \pm 1.6	37	14.4 \pm 2.2
26	Yanneymoon	30° 43' 04"S; 118° 33' 24"E	0.44	5	70.8 \pm 18.4	6.0 \pm 0.8	24	9.6 \pm 0.9
27	Quanta Cutting	30° 51' 49"S; 118° 25' 46"E	11.28	5	92.2 \pm 20.0	12.8 \pm 3.8	29	13.6 \pm 1.4
28	Isoetes ⁴	30° 54' 11"S; 118° 33' 20"E	0.20	5	125.0 \pm 39.1	5.0 \pm 0.0	8	3.2 \pm 0.5
29	Weira	30° 59' 54"S; 118° 23' 13"E	26.84	5	53.0 \pm 19.5	49.6 \pm 19.5	26	13.4 \pm 1.2

South District										
30 Roe ⁴	Mt Walker	31° 59' 37"S; 118° 48' 40"E	1.52	4	81.0 ± 32.7	5.0 ± 0	7	3.0 ± 0.4		
31 Twine Far North ⁴	Mt Walker	32° 06' 26"S; 118° 57' 22"E	0.14	4	96.0 ± 46.0	5.0 ± 0	8	3.5 ± 0.3		
32 Twine North	Mt Walker	32° 06' 34"S; 118° 57' 27"E	0.35	5	86.8 ± 14.3	19.3 ± 11.1	13	5.0 ± 0.3		
33 Twine Mid	Mt Walker	32° 06' 51"S; 118° 57' 27"E	4.05	5	162.2 ± 28.9	5.3 ± 0.3	18	6.8 ± 0.9		
34 Twine Shrub ²	Mt Walker	32° 06' 53"S; 118° 57' 27"E	0.47	5	475.0 ± 102.6	11.6 ± 2.3	16	5.8 ± 0.7		
35 Twine Southeast ²	Mt Walker	32° 06' 53"S; 118° 57' 28"E	1.35	5	88.4 ± 15.3	19.6 ± 1.3	18	7.4 ± 0.5		
36 Humps North	Hyden	32° 18' 41"S; 118° 57' 37"E	0.86	5	67.0 ± 10.9	16.4 ± 2.5	23	7.6 ± 0.9		
37 Humps South	Hyden	32° 18' 46"S; 118° 57' 38"E	0.25	5	84.6 ± 1.1	5.0 ± 0	12	5.6 ± 0.5		
38 Meeking ³	Hyden	32° 12' 53"S; 119° 05' 04"E	0.15	4	273.6 ± 57.0	5.0 ± 0	11	3.5 ± 0.6		
39 Wheelers ³	Hyden	32° 19' 59"S; 119° 17' 10"E	0.04	4	39.3 ± 26.1	5.0 ± 0	5	1.8 ± 0.5		
40 Boehm	Hyden	32° 21' 34"S; 119° 12' 02"E	0.44	4	69.6 ± 26.2	26.6 ± 23.5	14	7.2 ± 0.9		
Southeast District										
41 Forestiana North ¹	Hyden	32° 24' 42"S; 119° 12' 03"E	0.06	4	150.2 ± 42.6	19.2 ± 7.4	14	9.2 ± 1.3		
42 Forestiana South ³	Hyden	32° 24' 42"S; 119° 12' 03"E	0.07	4	129.6 ± 41.9	5.0 ± 0	5	1.5 ± 0.6		
43 Cave Rock ⁴	Widgiemooltha	31° 39' 40"S; 121° 13' 38"E	0.29	4	69.6 ± 6.0	5.0 ± 0	3	2.5 ± 0.3		
44 Higgensville North	Norseman	31° 44' 41"S; 121° 34' 08"E	2.08	4	150.0 ± 31.8	41.2 ± 7.3	16	11.2 ± 0.4		
45 Higgensville Mid	Norseman	31° 44' 41"S; 121° 34' 08"E	0.71	4	209.0 ± 46.4	38.0 ± 26.8	17	11.0 ± 0.7		
46 Higgensville South	Norseman	31° 44' 41"S; 121° 34' 08"E	0.19	4	105.2 ± 38.9	15.6 ± 6.4	12	7.0 ± 0.3		
47 Higgensville Southwest ³	Norseman	31° 44' 41"S; 121° 34' 07"E	0.24	4	114.0 ± 54.1	6.6 ± 1.4	8	5.0 ± 0.3		
48 Buldania East	Norseman	32° 07' 56"S; 120° 55' 38"E	2.48	4	207.0 ± 19.8	91.6 ± 12.7	21	14.0 ± 0.6		
49 Buldania South	Norseman	32° 07' 56"S; 120° 55' 38"E	0.43	4	159.4 ± 16.2	11.0 ± 3.3	13	7.8 ± 0.6		
50 Buldania West	Norseman	32° 07' 56"S; 120° 55' 37"E	1.99	4	449.4 ± 80.0	30.4 ± 8.4	17	8.2 ± 1.4		

¹ floods to greater area and depth² cleaned out November 2010³ capped⁴ lotic site